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Tree fern (Dicksoniaceae and Cyathaceae) allelopathy in the Monteverde cloud forest

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ABSTRACT

The purpose of this experiment was to look at the effects of Allelopathy between six species of tree ferns in the Monteverde Cloud Forest. We analyzed these effects by comparing plant abundances under the tree ferns to controls. We also compared controls to germination of seeds and spores grown with water or leachate made from the tree fern fronds. We found significantly higher plant abundances in controls than under the tree ferns. Also significantly less seed and spore germination than controls was found. There was not a significant difference between species of tree ferns in their inhibition of plants under the tree ferns. We did observe a difference in allelopathic effects on germinating tomato seeds and *Dicksonia gigantea* spores, though not for *Lophosoria quadripinnata* spores. These results lead us to conclude that Allelopathy in nature is affected by other factors such as facilitation or competition but different species of tree ferns do show differing levels of Allelopathy. Allelopathy in tree ferns inhibits spores more than seeds indicating that more closely related species inhibit each other more, at least in this case. Also we confirmed previous studies that found Allelopathy in tree ferns.

RESUMEN

El propósito de nuestro experimento debía mirar los efectos de alelopatía entre seis especies de helechos arborecentes. En el Bosque de Nube de Monteverde. Analizamos estos efectos comparando planta las abundancias bajo los helechos arborecentes a controles. Comparamos también los controles a la germinación de semillas y esporas crecidas con agua o leachate hizo de las trundas del helecho de árbol. Encontramos las abundancias apreciablemente más altas de planta en controles que bajo los helechos arborecentes. También apreciablemente menos germinación de semilla y espora que los controles se encontraron. No había una diferencia significativa entre la especie de helechos arborecentes en su inhibición de plantas bajo los helechos arborecentes. Observamos una diferencia en efectos de allelopathic a germinar las semillas de tomate y esporas de gigantea de Dicksonia, aunque no para esporas de quadripinnata de Lophosoria. Estos resultados nos dirigen a concluir ese allelopathy en la naturaleza es afectado por otros factores tales como facilitación o competencia pero la especie diferente de helechos arborecentes muestran difiriendo los niveles de allelopathy. También confirmamos los estudios previos que encontraron allelopathy en helechos arborecentes.

INTRODUCTION

Tree ferns are some of the world's oldest vascular plants and perhaps have survived for so long due to their allelopathic compounds. Allelopathy is the release of organic chemicals from one plant that causes the inhibition of germination, growth, or metabolism of a second plant. This form of interference within the plant community is distinct from competition, which acts through the depletion of resources (Del Moral and Gates 1971). However, the outcome of Allelopathy is similar to competitive exclusion in that it allows the plant that is releasing the secondary compounds to access more resources (Taiz and Zeiger 1991). Many studies on the effects of

Allelopathy have added to our understanding of the mechanisms that create community structure and thereby alter function and diversity of these plant communities (Callaway and Walker 1958). When a plant in a community influences others by altering the microhabitat and decreases the intrinsic rate of dispersal of other plants the community composition and structure is influenced (Harper 1977). For example *Camelina* spp. was found to cause a depression in the yield of *Linum usitatissimum* (Grümmer and Beyer 1960). Grümmer and Beyer found supporting evidence for this in an experiment in which *L. usitatissimum* was grown with its roots intermingled with *Camelina.* There was no inhibition of *L. usitatissimum* when the plants were watered from below the leaves, but a strong depression of L. *usitatissimum* was observed when watering was from above (Grümmer and Beyer 1960). This suggests that toxic chemicals of *Camelina* may play an integral role in the community composition.

The nature of allelopathic processes in tree ferns is somewhat unknown. An experiment by Kelly (2000) in the Monteverde Cloud Forest on tree ferns measured the observed effect of allelopathy and found a significantly lower diversity of plants downhill from tree ferns. This is perhaps a result of growth inhibiting compounds leaching downhill. The presence of allelopathic chemicals in tree ferns has also been supported by a study that found a lower germination rate in tomato seeds treated with a solution of tree fern pinnae, collected from plants of the *Alsophila* genus, and compared with a control of water (Duffield 1996). Both experiments support the existence of allelopathic compounds in tree fern fronds; however, it is still unknown if the degree of allelopathy differs between species in the strength of their effect.

Tree ferns have been found to have higher leaf turn over when they are healthy (Walker and Aplet 1994). If nearby plants are inhibited by fronds in the leaf litter as occurs around bracken ferns (Cooper-Driver 1990) there would be a stronger allelopathic effect under trees with a higher leaf turn over because there are more decaying fronds under them. If leaf turnover rate differs between species as local tree fern expert Denis Gomez stated (Personal Comunication 2003), this mechanism could lead to differences in allelopathy between tree fern species.

Tree ferns could also exhibit autopathy, the intra-specific inhibition of plant growth, germination and metabolism through the release of organic compounds. Some studies have been done on the effects of allelopathy and autopathy of ferns on spores. Davidonis and Ruddat completed a series of studies in 1973 that provided evidence supporting the inhibition of germination on their own and other fern spores by the non-tree fern *Tehlypteris normalis.* The levels of allelopathy on their own spores were found to be high in *T. normalis* (Daidonis and Ruddat 1973). This trend is what would be expected according to Lotka Voltera because two species occupying similar niches can co-exist if intra-specific competition is higher (Harper .1977). We assume that Allelopathy will function like competition in that it is a way of insuring more resources for one individual. Gomez (1983) is of the opinion that many pteridophytes show intra-specific inhibition and even target their own offspring. On the other hand, a study by Bell and Klikoff showed that not all fern species exhibit strong allelopathic effects on spore germination. This observation could be caused by secondary compounds acting like hormones which are inhibitors at high levels but at low levels promote growth (Bell and Klikoff 1976). Allelopathic compounds could also need the combined efforts of the tree fern's ability to compete for space and water to work effectively. It is possible that the conditions created underneath and around a tree fern create an environment that aids the allelopathic compounds in their inhibition of germination. It has been suggested that the magnitude of allelopathic effects of bracken ferns are amplified under stress conditions (Glass 1976). This observation could be a result of organic compounds acting together with the stressful conditions to create a synergism that inhibits the germination of surrounding plants (Bell and Klikoff 1976). If this is true the levels of

inhibition observed in a laboratory could be less than what is actually occurring in nature.

Here, we study the differences in the strength of autopathic and allelopathic effects of pinnae of different tree ferns species on spores, tomato seeds, and plant growth beneath the tree ferns. We hypothesize that there will be a difference between species in their strength of Allelopathy and their effects on both other tree ferns and plants in general. Based on previously cited observations (Gomez 1983), we predict that there will be high autopathic effects. Further more since closely related species tend to have similar requirements we predict that the more closely related species will have greater inhibition of each other.

MATERIALS AND METHODS

Study site and subject

This experiment was conducted in the lower montane wet rainforests behind la Estación Biológica de Monteverde along Sendero Principal and Sendero Cariblancos and in the Monteverde Cloud Forest Preserve along El Camino in Puntaranas, Costa Rica between October 17 and November 19 of 2003. We chose six common species of tree ferns and compared their allelopathic affects. These species were *Alsophila erinacea* var. *erinacea, Alsophila polystichoides, Cyathea caracasana* var. *meridensis,* and *Sphaeropteris brunei* in the family Cyatheaceae and *Dicksonia gigantea,* and *Lophosoria quadripinnata* in the family Dicksoniaceae. Tree ferns are gap specialists (Gomez 1983) so we chose trees near El Camino or in gaps so that light conditions and edge effects were similar. We also chose plants that did not have disturbances within a meter of their base, that were short enough that we could collect primary leaflets and that had access to their bases.

Leachate production

We studied ten individuals from each species taking 18.75 grams of leaf per plant, approximately two primary leaflets. To create leachate we used a similar method from a study done on allelopathy in *Alsophila* (Duffield 1996). We mixed the 18.75 grams of frond with 125 mL of distilled water in a blender to make a leachate of 0.15g primary leaflets per mL water. The leachate sat in a sealed container for two days to seep, after which we strained the solution using a wire mesh colander.

Spore growing experiment

We collected the spores from one individual of each tree fern species; these specimens were not necessarily individuals we used in our study. The fern spores were dried between sheets of paper for two days to allow the sori to open (Foster 1984). Each of the six species of spores was divided between 60 Petri dishes containing filter paper and 2.5 mL of leachate from one of the 60 plants sampled. Each species of tree fern spore also had a control with 2.5 mL of distilled water. These Petri dishes were then stored stacked in the windowsill where they each got the same amount of light for approximately two weeks.

Calculating spore germination

Dicksonia gigantea spores germinate after twelve days. We approximated the percent germination using a microscope and counted the percent germination in ten random eye views at ten times magnification. The *Lophosoria quadripinnata* spores started to germinate after fifteen days. Due to lack of time we had to count these before the control had completely germinated so

all the Petri dishes had less germination than the *D. gigantea* Petri dishes. Percent germination was approximated by scanning the dish for germination and counting the number of spores in the area surrounding the germinated spore. We always counted at least 100 spores, often more. Admittedly this method overestimated the percent germination, but the overestimation was consistent for all the samples. None of the other spores from the other species we used germinated during the time of our study.

Seed growing experiment
We also made Petri dishes of 20 tomato seeds, as evenly spaced as possible, using coffee filters and five mL of leachate for experimental dishes or five mL of distilled water for the control. We stored these in the dark (Duffield 1997) and checked the percent germination after four, five and eight days.

Transect abundance counts
Finally, we recorded the plant abundances of all ferns and vascular plants large enough to grow above the leaf litter in a one-meter square plot (50 cm on either side of the tree fern) directly downhill of the tree fern. We chose this method based on a paper by Kelly (2000), who found that only the downhill versus uphill plots with *Alsophila* showed a significant difference in the amount of Allelopathy. We used a light meter to measure the amount of light above the plot and then found a control plot nearby with the same light reading, on about the same slope and that was at least three meters from the nearest tree fern.

RESULTS

Plant abundances
The abundance of both non-fern plants and total plants was significantly higher in controls than under the tree ferns in many of the species *(D. gigantea* p = 0.0077 and 0.0069 respectively; *C. caracasana* p = 0.0051 for both A. *polystichoides* p = 0.0218 and 0.0128 respectively; *A. erinacea* p = 0.0499 and 0.0499 respectively. See tables 1, 2, 5 and 6 for the means and standard deviations). *L. quadripinnata* was only significantly different when total plant densities were used (mean 32.778 +/- 16.513 and controls mean 55.444 +/- 41.503 p = 0.0438. See table 3), and *S. brunei* was not significantly different but did show a general trend of having less angiosperms under the tree ferns than controls (mean 34.444 +/- 10.887 and control mean 42.778 +/- 5.449 p = 0.0658. See table 4).

None of the species of tree ferns showed statistically significant differences between the number of any pteridophyte underneath them and their controls (for means and standard deviations see tables 1 to 6).

ANOVA tests revealed no significant differences between the number of plants under different species of tree fern when the tests were run using direct counts or the abundances under tree ferns divided by their controls which we refer to as amount of inhibition, the higher the number the lower the inhibition. There were significantly more plants under *S. brunei* than under D. *gigantea* when the numbers of non-fern plants and total plants were compared *(D. gigantea* mean 21.4 plants +/- 7.0; and mean 22.3 plants +/- 6.865 respectively; *S. brunei* mean 34.444 +/- 10.887 and 36.222+/-11.155 respectively; p = 0.0156 and 0.0111 respectively); however, this significance was lost when comparing the inhibition. We did see that *D. gigantea* had the greatest inhibition of both angiosperms and total plants (mean 0.642 +/- 0.211 and 0.637 +/- 0.212. See table 1).

Seed germination

The seed samples were counted three times, once after four days, once after five days and once after eight days. We will refer to these hence forth as seed sample one, two or three based on how soon after preparation they were counted. We found that for most species of tree fern the percent germination of seed samples two and three were significantly less than in controls *(D. gigantea* p = 0.0284 and 0.0173 respectively; A. *polystichoides* p = 0.0033 and 0.0074 respectively; A. *erinacea* p = 0.0437 and 0.0116 respectively. See tables 1,5 and 6 for means and standard deviation). For *C. caracasana* all three samples were significantly less than controls (mean 0.262 +/- 0.071 and control mean 0.358 +/- 0 p = 0.0117; mean 0.361 +/- 0.057 and control mean 0.579 +/- 0 p = 0.0077; and mean 0.587 +/- 0.095 and control mean 0.790 +/-0 p = 0.0077, respectively. See table 2). *S. Brunei* was significantly different only in samples one and two (mean 0.196 +/- 0.159 and control mean 0.368 +/- 0 p = 0.0247; and mean 0.388 +/- 0.173 and control mean 0.579 +/- 0 p = 0.0116. See table 3). *L. quadripinnata* did not show significant inhibition of tomato seed germination.

There was a significant difference between the species of tree ferns' inhibition of tomato seed germination after samples two and three, inhibition is calculated by dividing each percent germination by the control, (p = 0.0437 and 0.0116 respectively, see figures 4 and 5. See tables 1 through 6 for means and standard deviations). C. caracasana and A. polystichoides inhibited the tomato seeds the most and A. erinacea and L. quadripinnata inhibited them the least. The control was the same for all individuals at each sample period. Sample one was not significantly different between species of tree fern.

Spore germination

Nearly all the tree ferns significantly decreased the amount of germination of *D. gigantea* spores (D. *gigantea* p = 0.0218, *S. Brunei* 0.0125, *L. quadripinnata* p = 0.0051, A. *polystichoides* p = 0.0164, *A. erinacea* p = 0.0058. See tables 1 and 3 through 6 for the means and standard deviation). *C. caracasana* did not show a significant difference from the control.

D. gigantea spore germination showed statistically significant differences between the six species of tree ferns when we compared inhibition (p < 0.0001 see figure 1. See tables 1 through 6 for means and standard deviations). We see that *L. quadripinnata* had the most inhibition of *D. gigantea* spores since it has the lowest mean inhibition number. C. carasana and A. polystichoides had the least amount of inhibition.

All tree fern species had lower *L. quadripinnata* percent germination than controls (D. *gigantea* p = 0.0051, *C. caracasana* p = 0.0077,5. *brunei* p = 0.0051, *L. quadripinnata* p = 0.0051, A. *polystichoides* p = 0.0033, A. *erinacea* p = 0.0033. See figures 1 through 6 for means and standard deviations).

There was no significant difference between amount of inhibition of *L. quadripinnata* spore germination between species (p = 0.1068. See figure 2). However, we did observe that *D. gigantea* leachate inhibited their germination the most (mean 0.115 +/- 0.144. See table 1). A. *polystichoides* had the least amount of inhibition.

For the two species with successful spore experiments we found a trend of autopathy. Both species had strong effects of inhibition on their own spores compared to the other species excluding their effects on each other (See figures 1 and 2).

Germination comparisons

The inhibition, percent germination of treatment divided by the control, of the sample three seed germination (mean 0.885 +/- 0.185) was significantly lower than the inhibition of

germination in either spore species ($p < 0.0001$), Recall that higher numbers represent less inhibition. Also *D. gigantea* spores (mean 0.579 +/- 0.371) had a significantly lower inhibition than *L quadripinnata* spores (mean 0.057 +/- 0.093, $p < 0.001$. See figure 3).

DISCUSSION

We demonstrated allelopathy in tree fern species through plant abundances versus controls, percent tomato seed germination versus controls and *L. quadripinnata* and *D. gigantea* percent spore germination versus controls. This study supports previous findings that tree ferns in the Monteverde Cloud Forest exhibit allelopathy (Duffield 1997, Kelly 2000). Previous studies in the area only looked at tree ferns in the genus *Alsophila* (Duffield 1997, Kelly 2000) while we demonstrated allelopathy in six species in two different families.

Angiosperm abundances and total plant abundances indicated allelopathy in tree ferns. This effect was not significantly different between species, which does not support our hypothesis that tree ferns vary in their amount of allelopathy. However, we did find a significant difference between species on their effect on tomato seed and *Dicksonia gigantea* spore germination, which does support our hypothesis. Together these results could indicate that tree fern species do have differing amounts of allelopathy but that the effects of this allelopathy are complicated by other factors in a natural setting. In Hawaii, Callaway and Walker (1997) found that some species of trees have both positive and negative effects on each other. The invasive *Myrica* tree provides nitrogen enrichment and shade for the local tree *Metrosideros*, however, leaf litter and root competition physically inhibit survival and growth underneath the tree for net negative effect on *Metrosideros.* Some form of facilitation by tree ferns could decrease the realized effect that allelopathic compounds have on surrounding plants. Lack of significant differences in allelopathy, observed as plant abundances, between species might also have been caused by less competitive ability in tree ferns that have higher amounts of allelopathy. Species of tree fern that spend a lot of energy on making more potent allelopathic compounds would have less energy available for growth of roots, stems or trunks or resource uptake adaptations. Species with more energy for growth and uptake of resources could have better competitive ability, but they would also have more plants to compete with because their allelopathy is less effective. The plants may divide their energy in different ways but the effects in nature may be equivalent. It is also possible that species with higher leaf turnover have either less allelopathic compounds per frond or have less potent allelopathic compounds because they have to replenish the compounds more frequently. However, since these species have more leaf matter under them they could still have a high concentration of compounds in the soil. For example *D. gigantea*, which can be identified by its skirt of dead fronds, showed the greatest amount of inhibition of angiosperms and all vascular plants, however it was average in its effect on germinating tomato seeds. These trends could indicate that *D. gigantea* amplifies its allelopathic effect by retaining its fronds so that they leach onto the soil for a longer period of time by slowing frond decomposition and keeping the frond in its vicinity. These arguments could explain why we did not see significant differences between the abundances of plants under different species even though we did observe differing amounts of allelopathy in laboratory settings.

Our hypothesis that autopathy was highest was not supported. However, we did find a trend toward high autopathy. This trend could explain the existence of many different species of tree ferns in similar niches. These findings conform with Lotka Voltera's theory that for two species to exist in the same realized niche there needs to be a higher amount of intra-specific

inhibition versus inter-specific. Since allelopathy is not competition but a way to decrease competition it is possible that the autopathy is accompanied by intra-specific competition. Our finding that autopathy was not higher than allelopathy could have been due to insignificant differences between the effects of different species' leachate on *L. quadripinnata* spore germination. The lack of a significant difference could be due to slower germination of L. *quadripinnata* spores so that they did not germinate completely during our study.

Another speculation is that autopathy could be a side effect of allelopathy. Tree fern species could have evolved allelopathic compounds to inhibit related species and inhibited themselves due to the similarities in spore structure and germination patterns. This explanation could explain the observed relationship of inhibition between *D. gigantea* and *L. quadripinnata* in that they both exhibited the strongest effects of inhibition on each other's spores. It should be noted that because there was no statistically significant difference between the effects of different species on *L. quadripinnata* spores the observation that D. *gigantea* had the strongest effect could still be questioned. This trend could be a ghost of allelopathy past The compounds may have evolved in the ancestors of these two Dicksoniaceae to inhibit each other to decrease direct competition. The progeny may have kept these compounds due to lack of pressure to change them. It could be that the autopathy, although potentially unintentional, helps the tree ferns by not allowing young tree ferns destined to die in the shade of the parent to steal resources from that parent or other siblings nearby. Furthermore, if allelopathic compounds really do function as hormones as Bell and Klikoff (1976) suggest then these compounds could enhance the survival of progeny that are far enough from the parent plant to not be in competition. The allelopathic compounds would be diluted at this distance from the parent plant so that they would promote germination or growth. This explanation could be tested by looking at the composition of allelopathic compounds and how they differ in relation to phylogenetic trees. Also experiments on how spores are affected by different concentrations of allelopathic compounds would be needed to prove or disprove their facilitory effects at low concentrations. Also larger spore growing experiments under allelopathic conditions are needed to confirm the trends we reported.

We found that there was more inhibition of spore germination compared to tomato seed germination. These differences were determined by dividing the percent germination in treatments by controls. This could be due to a higher need for inhibition of closely related species because they occupy similar niches and have evolved together for long periods of time. It is also important to remember that tomato plants do not grow in proximity of tree ferns. Therefore the allelopathic compounds may not have evolved to target these plants. There was inhibition of the seeds tested suggesting that the compounds have a negative effect on plants in general as has been previously shown (Duffield 1997).

We found that generally the seeds were not significantly inhibited until five days after the Petri dishes were prepared. This result could indicate that allelopathy on the seeds works by permanently inhibiting some seeds rather than by slowing down the growth of most or all seeds. The benefit of this form of allelopathy to the tree fern is obvious as it keeps the number of plants around it low by decreasing the number of seeds that can germinate. The one exception that we found was that S. *brunei* was only significantly different from controls in the seed germination samples one and two. In this species allelopathy may work by slowing down the germination of some plants. This strategy would make the seeds and seedlings more prone to predation and herbivores before they are able to actually compete with *S. Brunei* individuals.

Allelopathy is a very complicated plant interaction that is involved in the processes

of facilitation and competition, perhaps more than previously thought. We know that facilitation and competition are two major processes in determining community structure and composition. Once further information is found on the complex details of how allelopathic compounds affect these processes, the role of allelopathy in changing community composition can be understood.

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Table 1. Descriptive statistics for Dicksonia gigantean of all parameters. The plant counts are given in direct counts unless it says percent of control, which is the percent germination of the treatment divided by control. Seed and spore data are given in percent germination or inhibition, shown as percent control.

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum
Angiosperms under treefern	21.400	7.011	2.217	10	12.000	34.000
Angiosperms in controls	33.700	4.855	1.535	10	22.000	37.000
% control angiosperms	.642	.211	.067	10	.333	1.000
Fern under tree fern	.900	.876	.277	10	0.000	2.000
Fern in control	2.200	1.751	.554	10	0.000	4.000
Total plants under	22.300	6.865	2.171	10	14.000	36.000
Total plants control	35.900	6.244	1.975	10	22.000	41.000
% total plants control	.637	.212	.067	10	.350	1.036
Seed # sample 1	.251	.162	.051	10	.053	.632
Seed control sample 1	.368	0.000	0.000	10	.368	.368
Seed % control sample 1	.682	.440	.139	10	.143	1.714
Seed # sample 2	.429	.155	.049	10	.263	.684
Seed control sample 2	.579	0.000	0.000	10	.579	.579
Seed % control sample 2	.742	.267	.085	10	.455	1.182
Seed # sample 3	.689	.112	.035	10	.526	.842
Seed control sample 3	.790	0.000	0.000	10	.789	.789
Seed % control sample 3	.873	.142	.045	10	.667	1.067
D. gigantea #	.461	.393	.124	10	.009	.977
D. gigantea control	.911	.035	.011	10	.871	.986
D. gigantean % control	.510	.435	.137	10	.009	1.043
L. quadripinnata #	2.900E-4	.001	2.900E-4	10	0.000	.003
L. quadripinnata control	.146	.092	.029	10	.039	.218
L. quadripinnata % control	.007	.024	.007	10	0.000	.075

Table 2. Descriptive statistics for Cyathea caracasana showing all the factors we studied. The plant counts are given in direct counts unless it says percent of control, which is the percent germination of the treatment divided by control. Seed and spore data are given in percent germination or inhibition, shown as percent control.

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum
Angiosperms under treefern	29.600	11.862	3.751	10	5.000	47.000
Angiosperms in controls	43.700	7.832	2.477	10	34.000	58.000
% control angiosperms	.660	.214	.068	10	.147	.911
Fern under tree fern	2.500	1.269	.401	10	0.000	4.000
Fern in control	4.300	2.058	.651	10	0.000	6.000
Total plants under	32.100	12.050	3.811	10	7.000	50.000
Total plants control	48.000	8.138	2.573	10	37.000	58.000
% total plants control	.654	.197	.062	10	.189	.862
Seed # sample 1	.262	.071	.024	9	.150	.368
Seed control sample 1	.368	0.000	0.000	10	.368	.368
Seed % control sample 1	.712	.193	.064	9	.407	1.000
Seed # sample 2	.361	.057	.019	9	.300	.474
Seed control sample 2	.579	0.000	0.000	10	.579	.579
Seed % control sample 2	.623	.099	.033	9	.518	.818
Seed # sample 3	.587	.095	.032	9	.474	.737
Seed control sample 3	.790	0.000	0.000	10	.789	.789
Seed % control sample 3	.744	.120	.040	9	.600	.933
D. gigantea #	.711	.224	.075	9	.258	.930
D. gigantea control	.897	.051	.017	9	.871	.986
D. gigantean % control	.804	.274	.091	9	.262	1.068
L. quadripinnata #	.003	.003	.001	9	0.000	.009
L. quadripinnata control	.039	0.000	0.000	9	.039	.039
L. quadripinnata % control	.065	.089	.030	9	0.000	.243

Table 3. Descriptive statistics for Sphaepopteris brunei showing all the factors of this study. The plant counts are given in direct counts unless it says percent of control, which is the percent germination of the treatment divided by control. Seed and spore data are given in percent germination or inhibition, shown as percent control.

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum
Angiosperms under treefern	34.444	10.887	3.629	9	18.000	51.000
Angiosperms in controls	42.778	5.449	1.816	9	30.000	46.000
% control angiosperms	.825	.329	.110	9	.474	1.500
Fern under tree fern	1.778	1.787	.596	9	0.000	6.000
Fern in control	.556	1.333	.444	9	0.000	4.000
Total plants under	36.222	11.155	3.718	9	20.000	52.000
Total plants control	43.333	5.339	1.780	9	31.000	47.000
% total plants control	.861	.358	.119	9	.526	1.645
Seed # sample 1	.196	.156	.049	10	0.000	.579
Seed control sample 1	.368	0.000	0.000	10	.368	.368
Seed % control sample 1	.530	.425	.135	10	0.000	1.571
Seed # sample 2	.388	.173	.055	10	0.000	.579
Seed control sample 2	.579	0.000	0.000	10	.579	.579
Seed % control sample 2	.670	.299	.095	10	0.000	1.000
Seed # sample 3	.752	.148	.047	10	.421	1.000
Seed control sample 3	.790	0.000	0.000	10	.789	.789
Seed % control sample 3	.952	.188	.059	10	.533	1.267
D. gigantea #	.663	.196	.062	10	.399	.948
D. gigantea control	.908	.020	.006	10	.871	.918
D. gigantean % control	.730	.218	.069	10	.434	1.033
L. quadripinnata #	.018	.024	.008	10	0.000	.064
L. quadripinnata control	.182	.075	.024	10	.039	.218
L. quadripinnata % control	.082	.112	.035	10	0.000	.292

Table 4. Descriptive statistics for Lophosoria quadripinnata of all parameters we tested. The plant counts are given in direct counts unless it says percent of control, which is the percent germination of the treatment divided d by control. Seed and spore data are given in percent germination or inhibition, shown as percent control.

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum
Angiosperms under treefern	31.222	15.538	5.179	9	13.000	63.000
Angiosperms in controls	53.556	41.603	13.868	9	17.000	150.000
% control angiosperms	.768	.446	.149	9	.327	1.500
Fern under tree fern	1.556	1.667	.556	9	0.000	5.000
Fern in control	1.889	1.616	.539	9	0.000	5.000
Total plants under	32.778	16.513	5.504	9	14.000	68.000
Total plants control	55.444	41.503	13.834	9	20.000	153.000
% total plants control	.739	.386	.129	9	.338	1.480
Seed # sample 1	.295	.129	.041	10	.053	.421
Seed control sample 1	.368	0.000	0.000	10	.368	.368
Seed % control sample 1	.800	.351	.111	10	.143	1.143
Seed # sample 2	.484	.168	.053	10	.210	.737
Seed control sample 2	.579	0.000	0.000	10	.579	.579
Seed % control sample 2	.837	.290	.092	10	.364	1.273
Seed # sample 3	.774	.102	.032	10	.632	1.000
Seed control sample 3	.790	0.000	0.000	10	.789	.789
Seed % control sample 3	.980	.130	.041	10	.800	1.267
D. gigantea #	.113	.151	.048	10	0.000	.485
D. gigantea control	.918	0.000	0.000	10	.918	.918
D. gigantean % control	.123	.164	.052	10	0.000	.528
L. quadripinnata #	.005	.007	.002	10	0.000	.017
L. quadripinnata control	.218	0.000	0.000	10	.218	.218
L. quadripinnata % control	.025	0.033	.010	10	0.000	.079

Table 5. Descriptive statistics for Alsophila polystichoides of all the parameters we examined. The plant counts are given in direct counts unless it says percent of control, which is the percent germination of the treatment divided by control. Seed and spore data are given in percent germination or inhibition, shown as percent control.

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum
Angiosperms under treefern	31.273	11.577	3.490	11	14.000	58.000
Angiosperms in controls	59.273	34.555	10.419	11	16.000	135.000
% control angiosperms	.717	.559	.169	11	.269	2.188
Fern under tree fern	1.091	1.758	.530	11	0.000	5.000
Fern in control	2.364	2.111	.636	11	0.000	6.000
Total plants under	32.364	12.201	3.679	11	14.000	62.000
Total plants control	61.636	34.546	10.416	11	22.000	139.000
% total plants control	.658	.402	.121	11	.259	1.591
Seed # sample 1	.245	.211	.064	11	0.000	.763
Seed control sample 1	.368	0.000	0.000	11	.368	.368
Seed % control sample 1	.666	.572	.173	11	0.000	2.072
Seed # sample 2	.333	.139	.042	11	.105	.474
Seed control sample 2	.579	0.000	0.000	11	.579	.579
Seed % control sample 2	.576	.240	.072	11	.182	.818
Seed # sample 3	.624	.142	.043	11	.474	.842
Seed control sample 3	.790	0.000	0.000	11	.789	.789
Seed % control sample 3	.790	.180	.054	11	.600	1.067
D. gigantea #	.731	.206	.062	11	.290	.985
D. gigantea control	.907	.035	.011	11	.871	.986
D. gigantean % control	.804	.218	.066	11	.333	1.073
L. quadripinnata #	.010	.010	.003	11	0.000	.033
L. quadripinnata control	.136	.093	.028	11	.039	.218
L. quadripinnata % control	.115	.144	.046	10	0.000	.408

Table 6. Descriptive statistics for Alsophila erinacea of all parameters investigated. The plant counts are given in direct counts unless it says percent of control, which is the percent germination of the treatment divided d by control. Seed and spore data are given in percent germination or inhibition, shown as percent control.

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum
Angiosperms under treefern	27.083	10.388	2.999	12	14.000	49.000
Angiosperms in controls	35.417	14.656	4.231	12	14.000	66.000
% control angiosperms	.952	.837	.242	12	.273	3.500
Fern under tree fern	2.083	1.676	.484	12	0.000	5.000
Fern in control	1.917	2.778	.802	12	0.000	9.000
Total plants under	28.333	9.159	2.644	12	14.000	42.000
Total plants control	37.333	13.885	4.008	12	23.000	68.000
% total plants control	.836	.389	.112	12	.309	1.826
Seed # sample 1	.273	.145	.044	11	.105	.474
Seed control sample 1	.368	.0.000	0.000	12	.368	.368
Seed % control sample 1	.740	.393	.118	11	.286	1.286
Seed # sample 2	.531	.198	.060	11	.263	.842
Seed control sample 2	.579	0.000	0.000	12	.579	.579
Seed % control sample 2	.917	.341	.103	11	.455	1.455
Seed # sample 3	.756	.175	.053	11	.474	.947
Seed control sample 3	.790	0.000	0.000	12	.789	.789
Seed % control sample 3	.958	.222	.067	11	.600	1.200
D. gigantea #	.451	.320	.096	11	.062	.936
D. gigantea control	.901	.024	.007	11	.871	.918
D. gigantean % control	.509	.371	.112	11	.068	1.075
L. quadripinnata #	.004	.006	.002	11	0.000	.017
L. quadripinnata control	.153	.090	.027	11	.039	.218
L. quadripinnata % control	.046	.076	.023	11	0.000	.251

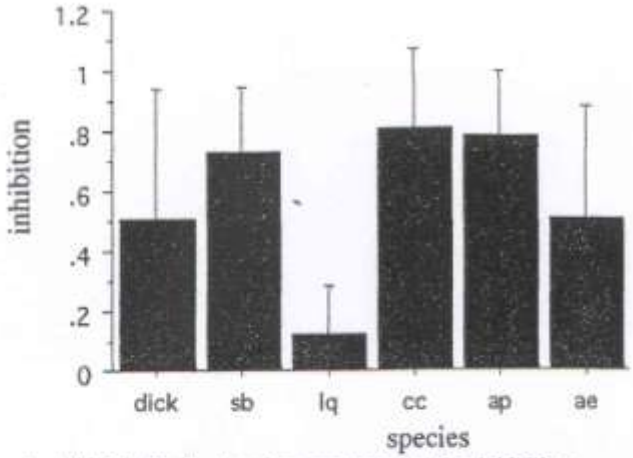

Figure 1. ANOVA for *D. gigantea* spore germination inhibition
Mean inhibition measured by dividing the experimental germination rate for each species of tree fern and dividing by the control. Higher numbers represent less inhibition. The standard deviation is also given for each species of tree fern. N was nine to eleven. The p value for this ANOVA was $p > 0.0001$.

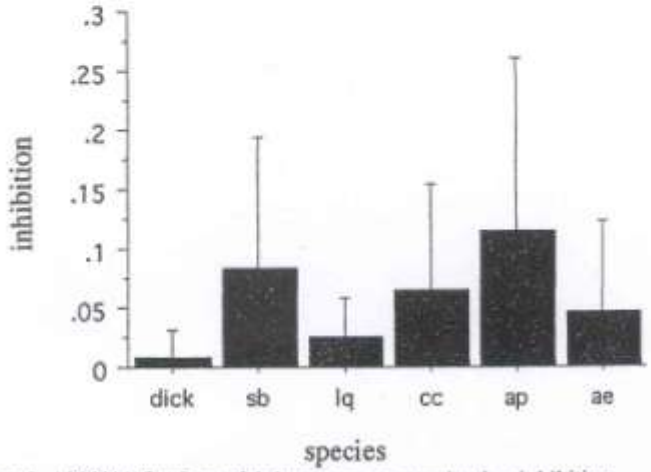

Figure 2. ANOVA for *L quadripinnata* spore germination inhibition
Mean inhibition measured by dividing the experimental germination rate for each species of tree fern and dividing by the control. Higher numbers represent less inhibition. The standard deviation is also given for each species of tree fern. N was nine to eleven. The p value for the ANOVA is $p = 0.1068$.

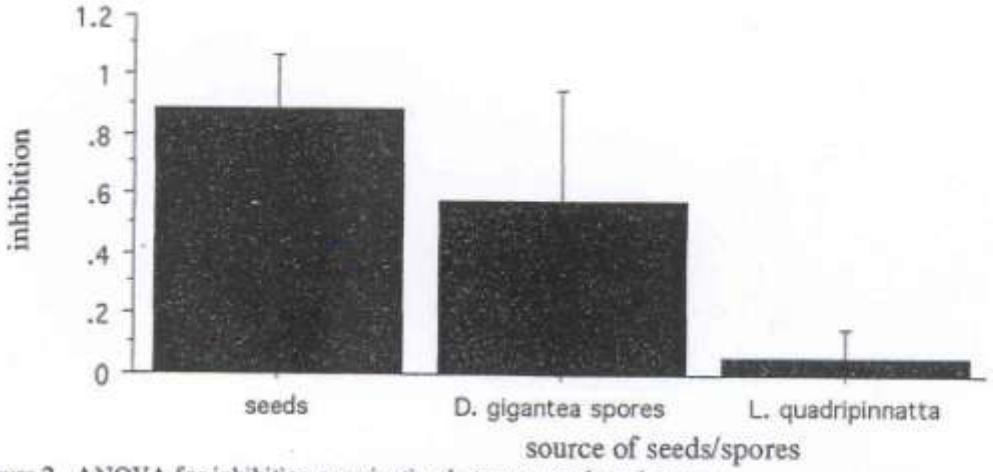

Figure 3. ANOVA for inhibition germination between seeds and spores
Inhibition was measured by dividing the percent germination in experimental samples by the controls. It shows the mean +/- SD for seed/ spore source. Inhibition is higher when the number is lower. Tomato seeds, *D. gigantea* and *L quadripinnata* spores were all significantly different. The ANOVA has $p > 0.0001$.

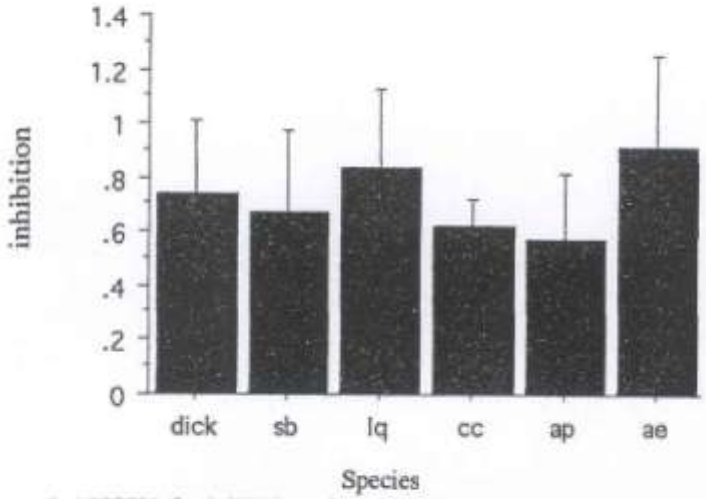

Figure 4. ANOVA for inhibition of germination of tomato seeds in sample two
Inhibition was measured by dividing the percent germination in experimental samples by the controls. It shows the mean +/- SD for each species. Inhibition is higher when the number is lower. These counts were made five days after seeds were prepared. N is nine to eleven and $p = 0.0437$.

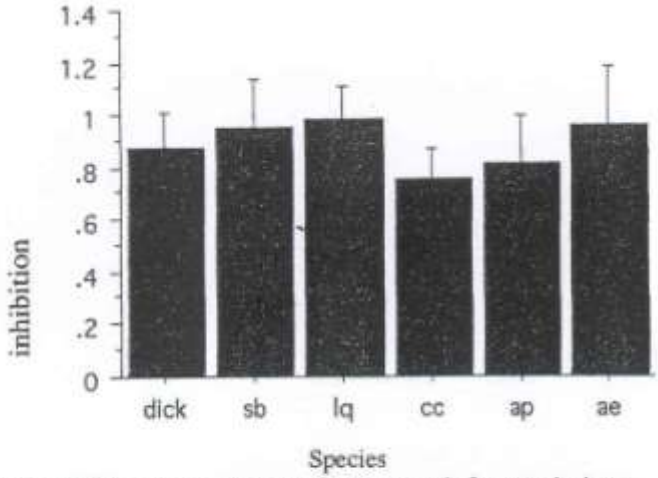

Figure 5. Inhibition of germination of tomato seeds for sample three
Inhibition was measured by dividing the percent germination in experimental samples by the controls. It shows the mean +/- SD for each species. Inhibition is higher when the number is lower. These counts were made eight days after seeds were prepared. N is nine to eleven and $p = 0.0116$.